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The effect of various environmental factors on the distribution of terrestric slugs (Gastropoda: Pulmonata: Arionidae) – An exemplary study

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A b s t r a c t : The study first considered the distribution of various arionids over the four subunits (two forests and two meadows) of a study area in the North of the city of Salzburg, Austria. In a second part, the influence of environmental factors on slug distribution was determined by the application of linear regression analysis. As exhibited by the results of the investigation, forests are preferred by all slug species as habitats due to their more appropriate climatic conditions and their higher cover of the ground with organic substrate. Differences of the total population densities between the four sub-units of the study area were partly highly significant ($p < 0.001$). Major determinants of slug distribution are emissive radiation, cover with moss, cover with herb plants, total shading, ground temperature, air temperature, and cover of the ground with litter. While *Arion ater/lusitanicus* seems to prefer habitats with increased moisture and medium temperatures, distribution of *A. fasciatus* agg., *A. subfuscus* agg., and *A. hortensis* agg. is probably less influenced by these factors, but much more by other parameters such as ground temperature, emissive radiation, and cover of the ground with litter.

K e y w o r d s : Environmental factor, distribution, linear regression analysis, slugs, Arionidae.

Introduction

During the past few decades, snails and slugs have increasingly occurred as major pests of a wide range of agricultural and horticultural crops (GODAN 1979, PORT & PORT 1986, SOUTH 1992, BARKER 2002). The damaging effect of slugs may be particularly recognized in temperate climates of Central and Northwest Europe, where partly huge armadas of gastropods dramatically reduce arable crops such as rape, sugar beet, and maize, but also certain kinds of vegetables (e.g. lettuce and numerous Brassicaceae) (GODAN 1979, SOUTH 1992). From an economic point of view, the most important slug species acting as pests in Central Europe are *Deroceras reticulatum* MÜLLER, belonging to the Agriolimacidae, *Arion lusitanicus* MABILLE and the *A. hortensis* aggregate, both belonging to the Arionidae. While *Deroceras reticulatum* is characterized by its occurrence in temperate regions all over the world (SOUTH 1992), *Arion lusitanicus* was originally endemic to the Iberian peninsula, but became distributed over Central Europe in recent years (FECHTER & FALKNER 1990, TURNER et al. 1998, SPEISER & KISTLER 2002). The *A. hortensis*

aggregate includes three species, being only discernible by their internal anatomy: 1) *A. hortensis* s.s., 2) *A. distinctus*, and 3) *A. owenii* (DAVIES 1977, 1979). Further slug species occurring in Central Europe but being less important in agronomic research are *A. ater* LINNAEUS, which reaches a similar size as *A. lusitanicus*, *A. subfuscus* agg. MÜLLER, and *A. fasciatus* agg. NILSSON (BOGON 1990, FECHTER & FALKNER 1990).

Studies concerning the regional distribution as well as distribution strategies of slugs have been frequently published in the open literature during the last 25 years (e.g WIESE 1985, KOZLOWSKI 2000, REISCHÜTZ 2000, IGLESIAS & SPEISER 2001, GRIMM & PAILL 2001). According to the investigations of GRIMM & PAILL (2001), slugs are believed to have home-ranges, i.e., areas of limited size which are not left by the animals during their adult life time. For *A. lusitanicus* home-range size is subject to significant fluctuations and depends among other on weather conditions and population densities. Studies describing the relationship between arionid species and their environment so far include few quantitative investigations, where the number of slugs has been determined within small vegetation areas (e.g. WALHOVD 1996, FRANK 1998, BRINER & FRANK 1998) and the relationship between gastropods and soil properties has been subject to a more detailed inspection (ONDINA et al. 2004). These latter studies could demonstrate that slugs either prefer wetter, finer-textured, less acidic soils (such as *Deroceras reticulatum*) or are rather indifferent to most edaphic factors (e.g. *Arion intermedius* NORMAND).

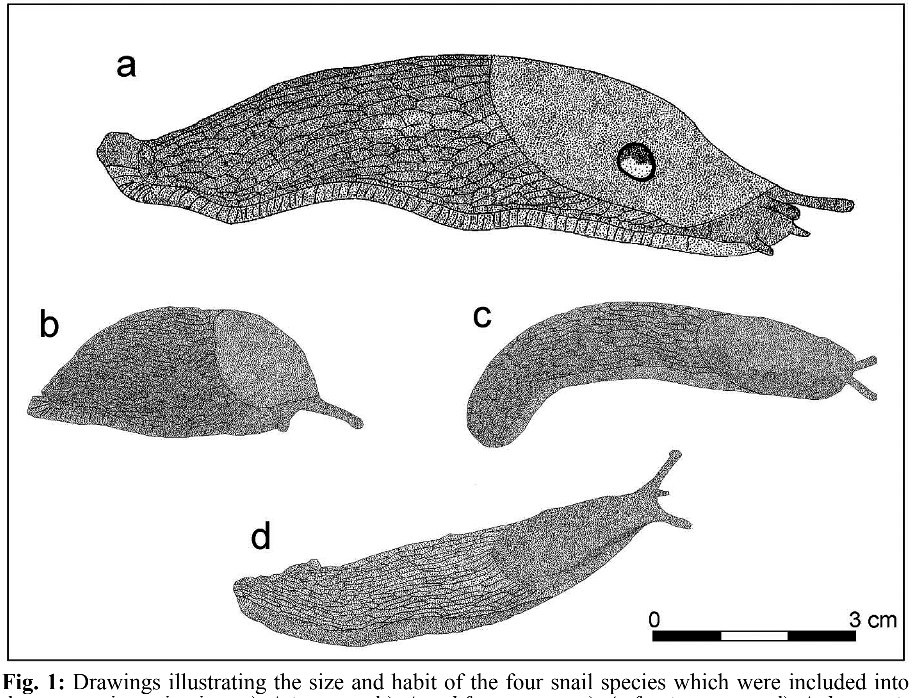

Fig. 1: Drawings illustrating the size and habit of the four snail species which were included into the present investigation: a) *Arion ater*, b) *A. subfuscus* agg., c) *A. fasciatus* agg., d) *A. hortensis* agg.

As the objective of the study presented here, the distribution of various species and species aggregates of the genus *Arion* (Fig. 1) is described in detail for four different vege-

tation areas (two forests and two meadows with different plant associations), using a specific strategy for animal counting. Distribution data obtained from the field research are processed statistically to decode (a) differences of population densities within a single vegetation area, (b) differences of population densities between the studied areas, and (c) possible relationships between environmental factors and the colonization of forests /meadows by arionids.

Materials and Methods

Experimental site

The study was conducted in a green belt in the North of the city of Salzburg. Field work including the counting of the molluscs, recording of plant associations, and measurement of diverse environmental factors was carried out in August 2000, whereby for statistical purposes sampling was repeated for five times. As illustrated in Fig. 2, the study area consists of four sub-units, i.e. two forests and two meadows. Forest 1 within the study area shows typical characteristics of a pasture woodland with high densities of *Fraxinus excelsior*, *Alnus incana*, *Acer pseudoplatanus*, and *Ulmus glabra*. In general, the vegetation of this sub-unit falls in the phytosociological association *Alno-Fraxinetum*.

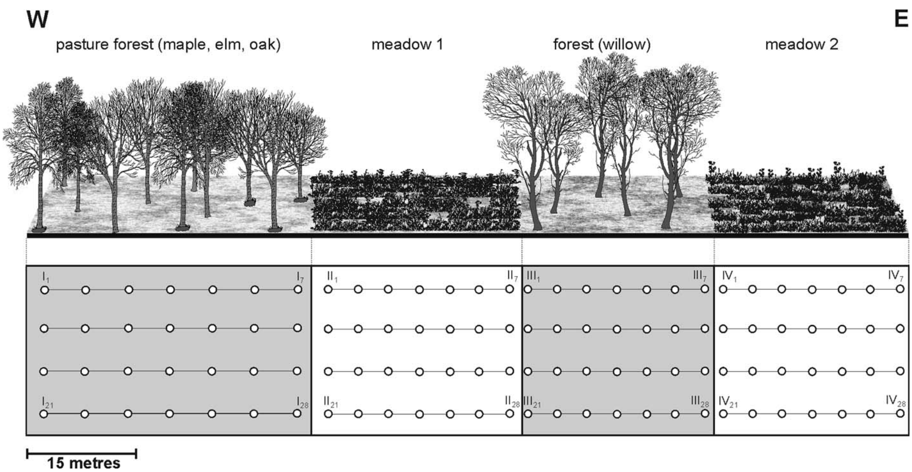

Fig. 2: Scheme illustrating the study area with its four sub-units. The area is characterized by the alternating sequence of small forests and meadows exhibiting a predominance of different plant associations, respectively. The sketch below shows the arrangement of single sample points within each of the four areas.

Concerning its vegetation, forest 2 differs significantly from forest 1, thereby mainly including species of the genus *Salix* and also a much smaller population of *Fraxinus excelsior*. Investigation of the plant association according to the method of Braun-Blanquet resulted in a total number of 67 plant species, most of which belong to the herb layer. The sub-unit may be assigned to the phytosociological class *Salicetea purpureae*. Regarding meadow 1, a total number of 57 plant species could be determined. Appearance of the character species *Arrhenatherum elatius*, *Crepis biennis*, *Campanula patula*, *Galium album*, and *Pimpinella major* allowed an assignment of this area to the phytosociological class *Molinio-Arrhenatheratea*. The meadow additionally includes several indicators of increased moisture, e.g. *Glechoma hederacea*, *Ajuga reptans*, *Alopecurus pratensis*, *Poa trivialis*, and, with lower frequency, *Carex hirta* and *C. sylvatica*. Meadow 2 exhibits some typical characteristics of a non-economically used grassland with tall-growing herb plants and dense cover of the soil with litter. Dominant plant species are among other *Urtica dioica*, *Artemisia vulgaris*, *Cirsium arvense*, and *Rumex obtusifolius*, allowing an assignment of the area to the phytosociological class *Artemisietea*. Characteristic grass species within the meadow are *Holcus lanatus*, *Fraxinus pratensis*, *F. gigantea*, *Poa pratensis*, and *P. trivialis*.

Mollusc counting and recording of environmental factors

The strategy for counting slugs within the sub-units of the study area is illustrated in the scheme of Fig. 2. Therefore, within each sub-unit sample points were arranged along four lines with a length of about 30 metres, respectively. For each line, seven sample points with equal interdistances were selected. Sampling took place on five days with different weather conditions, and sampling time ranged from 8^{00} a.m. to 5^{00} p.m. Counting of the arionids was conducted by using a frequency frame of 0.5 x 0.5 metres size and recording all slugs being within this frame at the respective sample points. For this, adult and juvenile animals of each slug species were carefully gathered by hand. Besides the surface and the plants within the frame, also the litter as well as the uppermost layer of the ground were probed for molluscs. Determination of single slug species was carried out by searching for specific characteristics (e.g. body colour, colour of the sole, mucus colour and size), being described by e.g. BOGON (1990) or FECHTER & FALKNER (1990).

Besides the recording of slug populations at each sample point, also environmental factors being considered as essential for this study were measured. These included air temperature (°C), relative humidity (%) 2 metres and 5 centimetres above the ground, shading directly above the ground (%), cover of the ground with litter, cover with herb, moss and bushes, ground temperature (°C) in 0 and 5 centimetres depth, evaporation (cm/h) directly above the ground, and emissive radiation (W/m²). While physical factors were recorded every hour over a period of nine hours (from 8^{00} a.m. to 5^{00} p.m.) for getting detailed information on their daily changes, biological factors (shading, litter, plant cover) were only measured once a day. For the analysis of shading, vertical light was assumed, whereas the cover of the ground by litter, moss, herb and bush plants was quantified by defining respective cover indices ranging from 0 (= 0 %) to 4 (= 100 %).

Data analysis

From the counting data obtained with the frequency frame method, population densities of single arionid species were expressed in terms of individuals per square metre. In general, four categories of slug species were distinguished, whereby *Arion lusitanicus* and *A. ater* were attributed to one category. Distribution maps of the molluscs were generated by application of a linear-kriging method. For exhibiting differences of (a) population densities between slug species within one sub-unit and (b) population densities between the sub-units for a given slug species, data were first tested according to their normality (i.e., if data can be explained by a normal distribution) and subsequently subject to respective testing statistics. Environmental factors were processed statistically by the calculation of mean values and standard deviations. Where necessary, differences of factors between the sub-units or within a sub-unit were tested in the same way as the slug counting data. Relationships between environmental factors and slug distribution were tried to be decoded by the application of linear regression analysis and the computation of related correlation coefficients.

Results

Determination of the arionid distribution

Results of slug counting and reconstruction of their distribution in the sub-units of the study area are summarized in Tab. 1 and Fig. 3. In Tab. 1 mean population densities expressed by individuals per square metre are listed for both the four species categories described in the previous section and the four sub-units. Depending upon species and sub-unit, population density ranges from 0 ind./m² (*A. subfuscus* agg. on meadow 1) to 3.21 $\pm$ 0.32 ind./m² (*A. hortensis* agg. in forest 1). Significant differences of the population densities between different species within a sub-unit have been recognized for all parts of the study area, whereby, according to a general tendency, *A. hortensis* agg. is most prominent in all sub-units, while *A. subfuscus* agg. occurs with lowest population densities (Tab. 1). Occurrences of single species categories may also be subject to significant discrepancies among the four sub-units of the study area. This is best shown by the comparison of forest and meadow, in the latter of which slug occurrences are characterized by partly dramatic decreases (Tab. 1). Generally, forest 1 keeps the highest number of slugs, whereas on meadow 1 overall population density is reduced to a minimum.

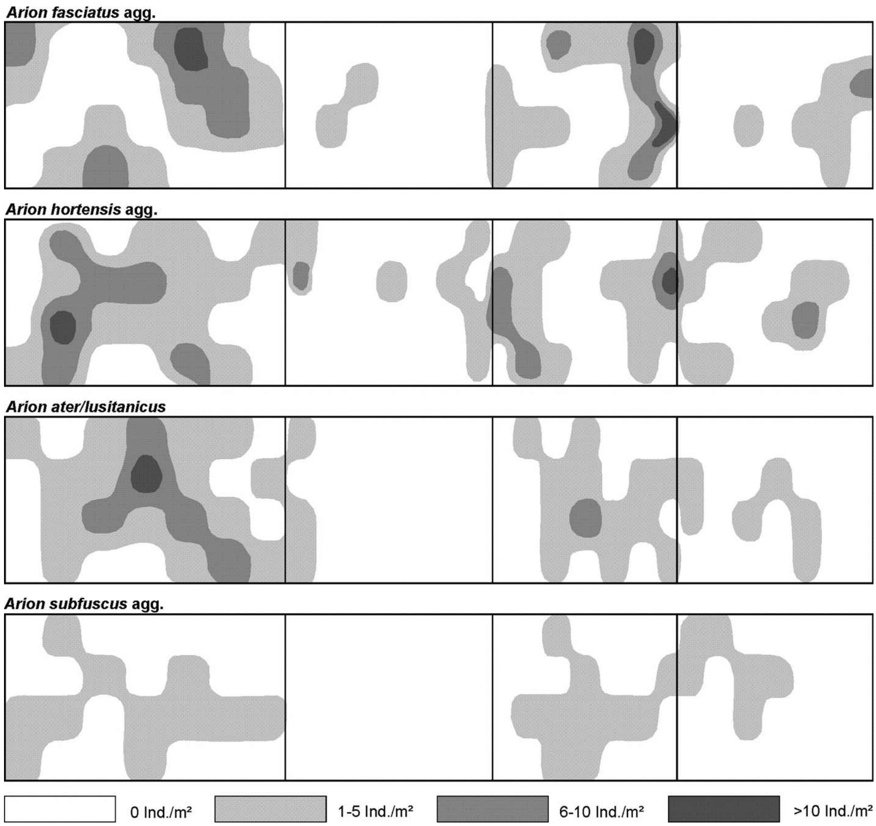

Fig. 3: Distribution maps for the slug groups investigated in this study. As clearly recognizable from the graphs, at the time of the investigation slug distribution within the forest areas is more highly developed with respect to that on the meadows.

Tab. 1: Individual density (ind./m²) of the studied slug species in the single areas introduced in Fig. 1. Significant differences (*: $p < 0.01$; **: $p < 0.001$) between the species within one area and between the areas ($^{+}$: $p < 0.01$; $^{++}$: $p < 0.001$) for one species are marked, respectively.

Species		forest 1	meadow 1	forest 2	meadow 2
A. fasciatus	mean	2.82	0.21	2.18	0.68
	stdev	0.28	0.02	0.22	0.07
A. hortensis	mean	3.21*	0.57**($^{++}$)	1.61*($^{++}$)	0.79^{++}
	stdev	0.32	0.06	0.16	0.08
A. lusitanicus/ater	mean	3.11	0.32**($^{++}$)	1.21**($^{++}$)	0.43*($^{++}$)
	stdev	0.31	0.03	0.12	0.04
A. subfuscus	mean	1.07**	----------	0.86**	0.43^{++}
	stdev	0.11	----------	0.09	0.04
Total	mean	2.55	0.37^{++}	1.46^{++}	0.58^{++}
	stdev	0.26	0.11	0.15	0.17

Slug distribution maps based on the counting raw data (Fig. 3) clearly underline the results provided above. Except for *A. subfuscus* agg., all species may occur with up to > 10 ind./m² in the forests, whereby this high population density has been recorded more frequently in forest 1. On meadow 1 arionids either do not occur at all or are marked by population densities of 1–5 ind./m². On meadow 2 excess of 5 ind./m² only occurs in very exceptional cases. Population densities are partly increased in the transition zones between meadow and forest (Fig. 2).

Environmental factors

Tab. 2: Biotic and abiotic factors measured in the single areas of Fig. 1. Significant differences between the areas are marked by $^{+}$ ($p < 0.01$) and $^{++}$ ($p < 0.001$), respectively. Concerning ground temperature in 0 and 5 cm depth, temperature differences were highly significant in all cases (**: $p < 0.001$).

Parameter		forest 1	meadow 1	forest 2	meadow 2
Temperature max. (° C)	mean	25.61	27.87^{+}	25.95^{+}	28.79^{+}
	stdev	1.16	1.28	0.93	0.92
Rel. Humidity (%)	mean	71.35	59.39^{+}	73.12^{+}	59.65^{+}
	stdev	4.32	7.91	3.15	9.05
Shading (%)	mean	79.28	82.5	61.22	78.72
	stdev	18.78	12.4	16.03	13.49
Litter (%)	mean	44.3	14.5^{+}	71.3^{+}	56.0
	stdev	18.8	20.8	18.8	20.3
Soil temperature	mean	25.42	29.3	28.36	30.84
(0 cm, ° C)	stdev	2.54	1.95	2.17	3.12
Soil temperature	mean	17.32**	20.56**$^{++}$	18.66**$^{+}$	18.25**
(5 cm, ° C)	stdev	0.34	0.48	0.78	0.54
Rel. Humidity	mean	68.6	62.3	74.5	48.5^{+}
(5 cm, %)	stdev	4.7	5.8	10.4	10.8
Evaporation (ml/h)	mean	0.23	0.36^{+}	0.25^{+}	0.38^{+}
	stdev	0.04	0.08	0.05	0.11
Emissive Rad. (W/m²)	mean	98	267^{++}	132^{+}	384^{++}
	stdev	28	75	34	86
Cover with herb (%)	mean	52.1	82.5^{+}	36.5^{++}	78.7^{++}
	stdev	18.8	12.4	14.1	13.5
Cover with bush (%)	mean	18.9	0.9^{++}	31.1^{++}	3.2^{++}
	stdev	13.3	0.2	16.0	1.1
Cover with tree (%)	mean	79.3	------	61.2	9.4^{++}
	stdev	14.7	------	12.9	1.8

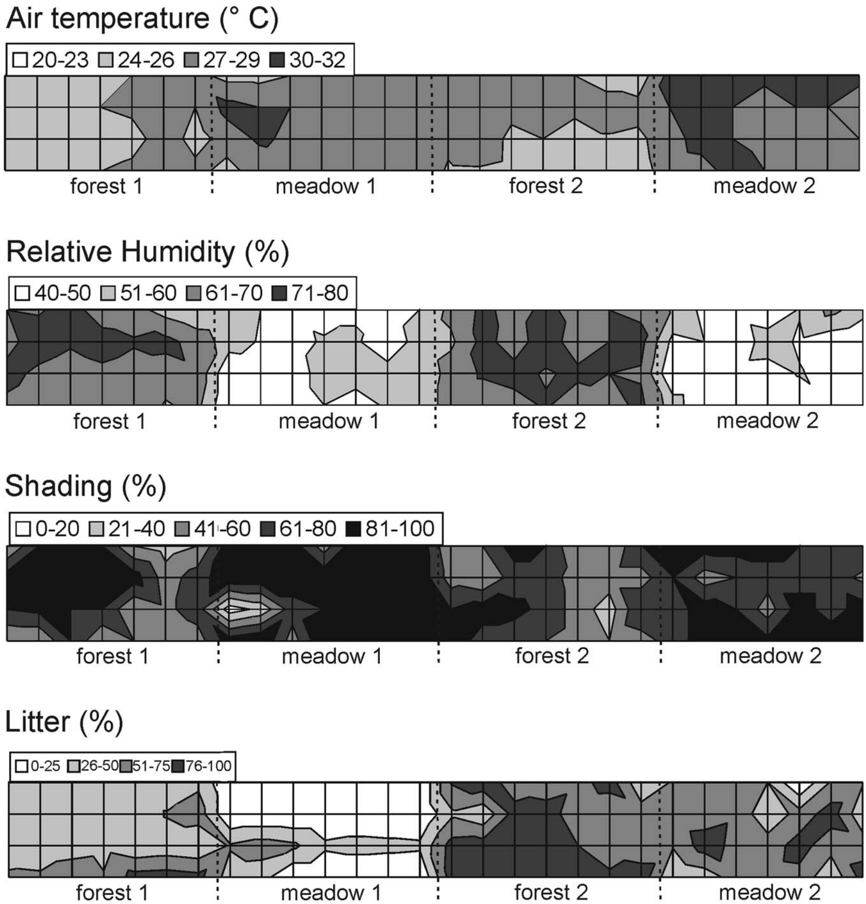

Fig. 4: Distribution maps of four environmental factors recorded in the study area.

Results of environmental factor analysis are listed in Tab. 2. Maximum air temperature measured at 1 p.m. ranges from 25.61 $\pm$ 1.16 °C in forest 1 to 28.79 $\pm$ 0.92 °C in meadow 2, thereby showing significant differences between the sub-units of the study area. While relative humidity is highest in forest 2 (73.12 $\pm$ 3.15 %), shading of the ground has a maximum on meadow 2 (82.5 $\pm$ 12.4 %). Concerning the cover of the ground with litter, forest 2 and meadow 2 exhibit highest values, whereas on meadow 1 deposition of plant rudiments on the ground is very limited due to the agricultural use of this greenland. In the forests, cover with moss and herb is increased with respect to the meadows. Ground temperature measured on the surface is insignificantly higher on the meadows than in the forests (Tab. 2). When measured in a depth of 5 centimetres, a highly significant drop of the temperature ranging from 8 to 12 °C can be recognized for all units of the study area, whereas temperature differences among the sub-units are on the same order of magnitude as determined for surface temperature. Evaporation rates show trends contrary to relative humidity, with maxima being discernible on the mead-

ows, respectively (0.38 ± 0.11 cm/h on meadow 2 vs. 0.36 ± 0.08 cm/h on meadow 1). The same phenomena can be observed for emissive radiation, where mean values measured on the meadows differ from those in the forests by a factor 2 – 3 (Tab. 2).

Distribution maps of selected environmental factors are illustrated in Fig. 4, visualizing most of the trends described above. Therefore, differences between forests and meadows are best observable for relative humidity, and agricultural use of meadow 1 is clearly underlined by the map of litter distribution.

Relationship between slug distribution and environmental conditions

Results of linear regression analysis for working out possible correlation between the distribution of slugs over the study area and selected environmental factors are summarized in Tab. 3. Concerning the computations carried out for each species aggregate, best correlation between individual density and independent variable could be decoded for air temperature (R^2: 0.67-0.94), soil temperature on the surface (R^2: 0.72-0.94), and evaporation (R^2: 0.72-0.96), while according to the presented results cover of the ground with litter (R^2: 0.03-0.28) and shading (R^2: 0.00-0.21) do not seem to have significant effects on the slug populations. As exhibited by the Pearson correlation coefficients listed in Tab. 3, negative correlation between population density and environmental variable could be determined for five cases and positive correlation for three cases. Differences between single species aggregates are most evident for litter index and shading, whereas trend lines obtained for the remaining environmental variables are partly very similar.

Tab. 3: Results of linear regression analyses which were carried out for each of the four species aggregates investigated in this study. As clearly recognizable from the single regression parameters, ecology of the studied slugs seems to be very similar. Most remarkable differences between the species aggregates could be found for litter index and shading (Abbreviations: Af = *Arion fasciatius* agg., Ah = *A. hortensis* agg., Ala = *A. lusitanicus/ater*, As = *A. subfuscus* agg.).

Environmental variable	Constant				Slope				Goodness-of-fit R²				Pearson correlation coefficient			
	Af	Ah	Ala	As	Af	Ah	Ala	As	Af	Ah	Ala	As	Af	Ah	Ala	As
air temperature	21.4	19.3	19.9	5.67	-0.73	-0.66	-0.69	-0.18	0.83	0.70	0.67	0.94	-0.91	-0.84	-0.82	-0.97
relative humidity, 50 cm	-8.9	-6.8	-7.2	-1.90	0.16	0.12	0.13	0.04	0.89	0.60	0.54	0.81	0.94	0.77	0.73	0.90
litter index	0.21	0.96	0.82	1.10	0.68	0.31	0.24	-0.15	0.28	0.06	0.03	0.07	0.53	0.24	0.17	-0.26
shading	5.9	2.6	1.7	1.16	-0.06	-0.01	-0.01	-0.01	0.21	0.01	0.00	0.03	-0.46	-0.10	0.00	-0.17
soil temperature, 0 cm	14.5	15.6	16.5	4.10	-0.46	-0.49	-0.54	-0.12	0.72	0.88	0.90	0.94	-0.85	-0.94	-0.95	-0.97
relative humidity, 5 cm	-3.3	-2.2	-2.6	-0.52	0.08	0.06	0.06	0.02	0.47	0.29	0.27	0.73	0.69	0.54	0.52	0.85
evaporation	6.2	5.8	5.7	1.90	-15.5	-13.8	-14.5	-3.9	0.92	0.77	0.72	0.96	-0.96	-0.88	-0.85	-0.98
emitted radiation	3.2	3.2	3.0	1.20	-0.01	-0.01	-0.01	0.00	0.74	0.64	0.63	0.95	-0.86	-0.80	-0.79	-0.97

Discussion

In the study presented here the distribution of various slug species was found to correlate with essential environmental factors. Comparison of population densities between the four sub-units of the study area, which was the first objective of the investigation, exhib-

ited significant differences between the forests, where partly high numbers of individuals per square metre could be recognized, and the meadows with partly no occurrence of arionids at all (Tab. 1). Studies on arionids published in the open literature have so far mainly focused on systematic problems, questions concerning distributions on a more regional scale, and the development of molluscicides for damming the dispersal of slugs over agricultural and horticultural areas. Relationships between slug distribution on a smaller scale and environmental factors have been only discussed marginally in the past (e.g. ROLLO 1983, SOUTH 1992, GRIMM & PAILL 2001). Regarding *Arion lusitanicus*, being a preferred model organism due to its rapid dispersal over Central Europe, SOUTH (1992) stated that shelter and population density can all influence slug dispersal. Also favourable microclimatic conditions throughout the season and closeness to feeding grounds were evaluated as highly important for habitats colonized by arionids, which is also supported in part by the present contribution (Tab. 3). In the literature adjacent food supply is believed to have a predominance over all other factors, since slugs are known to use up to 30 % of their energy budget for movement (WILLIAMSON & CAMERON 1976, DENNY 1980). If food supply is quantified by the cover of the ground with litter, the findings of SOUTH (1992) are underlined in part by this study, since linear regression exhibited a respective correlation between this factor and the population density of most slug species.

Concerning the occupancy of best shelters, slugs are normally subject to an interspecific competition, where very aggressive species usually dominate over the other species. In the literature, *A. subfuscus* agg. is described as such an aggressive arionid species (ROLLO & WELLINGTON 1979), highly influencing the distribution of other slugs. In the present study, however, population density of *A. subfuscus* agg. in the four sub-units of the study area is significantly lower with respect to the other species, and therefore genuine aggressiveness cannot be concluded from the results presented here (Tab. 1, Fig. 3). Similar results questioning the role of *A. subfuscus* agg. were outlined by GRIMM & PAILL (2001), where a clear predominance of *A. lusitanicus* over the other slug species was recorded on the site of investigation. The authors concluded that aggression is rather low for most of the life time in slug species and intraspecific density plays a more important role for the distribution of gastropods.

Migration and distribution of *A. lusitanicus* was studied by MÜLLER & OHNESORGE (1985) for a 12-day summer period. The authors could find out that the species is characterized by high vagility as well as a frequent change of resting places. Migration of the slug was attributed to hot weather conditions, which can be only supported in parts by the study due to limitation of slug sampling to five days. GRIMM & PAILL (2001) also discuss a possible dependence of the vagility of *A. lusitanicus* on its gender phase, because in its female phase the gastropod is most vagile. The authors further describe this species to be marked by high adaptive capacity and flexibility, being typical properties of colonizers, which are more commonly habitat generalists than specialists. Regarding migration activity in the study area of the present work, distributions illustrated in Fig. 2 suggest that *A. fasciatus* and *A. hortensis* agg. seem to show highest vagility. Finding reasons for this phenomenon would need to enter a speculative sphere, but factors coming into question may be a lower energy consumption for migrating, a more generalized behaviour concerning food consumption, etc.

The present study has tried to enlarge our knowledge on the distribution of terrestric

slugs in natural environments characterized by different climatic conditions and vegetation compositions. Although important results have been obtained by the application of classical mathematical methods, further investigations will be necessary to bring more light into this complex topic.

Zusammenfassung

Die Wirkung verschiedener Umweltfaktoren auf die Verbreitung terrestrischer Nacktschnecken (Gastropoda: Pulmonata: Arionidae) – Eine exemplarische Untersuchung. – Die Studie hatte die Untersuchung der Verbreitung verschiedener Arioniden in vier Untereinheiten (zwei Wälder und zwei Wiesen) eines Arbeitsareals im Norden der Stadt Salzburg (Österreich) zum Inhalt. In weiterer Folge sollte der Einfluss von Umweltfaktoren auf die Verbreitung der Nacktschnecken unter Verwendung der linearen Regressionsanalyse näher untersucht werden. Wie durch die Ergebnisse belegt wird, stellen die Wälder aufgrund ihrer geeigneteren klimatischen Bedingungen und der stärkeren Bedeckung des Bodens mit organischem Substrat die bevorzugten Habitate aller betrachteten Arten dar. Unterschiede der Gesamtpopulationsdichten zwischen den vier Einheiten des Arbeitsgebietes sind teilweise hochsignifikant ($p < 0.001$). Emittierte Strahlung, Deckung mit Moos und krautigen Pflanzen, Beschattung, Boden- und Lufttemperatur sowie die Bedeckung des Bodens mit organischer Streu scheinen die bestimmenden Faktoren für die Verbreitung der Schnecken darzustellen. Während *Arion ater/lusitanicus* Habitate mit erhöhter Feuchtigkeit und mittleren Temperaturen bevorzugt, haben diese Faktoren auf die Verbreitung von *A. fasciatus* agg., *A. subfuscus* agg. und *A. hortensis* agg. einen geringeren Effekt. Hier spielen wahrscheinlich andere Faktoren wie Bodentemperatur, emittierte Strahlung und Streubedeckung eine größere Rolle.

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